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A Historical Perspective on Recent Studies of Social Learning About Foods by Norway Rats

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ABSTRACT Early naturalists explained field observations of social influences on animal learning in terms of spoken language, deliberate tuition of one animal by another, or intentional imitation. During the first half of the present century, experimental psychologists analyzed instances of social learning by animals in laboratory tasks as special cases of operant or classical conditioning. Neither of these traditional approaches provided much insight into the complex processes that often support animal social learning. By combining ethological focus on social learning as it occurs in natural habitat with analytical techniques developed in the psychological laboratory, contemporary researchers have made considerable progress in describing the many ways in which social interactions influence behavioural development in animals. The author's investigations of social influences on food selection by Norway rats provide one example of such an ethopsychological approach to the study of animal social learning.

RÉSUMÉ Les premiers naturalistes expliquaient leurs observations sur le terrain quant aux influences sociales sur l'apprentissage animal en termes de langage parlé, de cours délibéré d'un animal à un autre ou d'imitation intentionnelle. Pendant la première partie de ce siècle-ci, les psychologues expérimentalistes analysaient les exemples d'apprentissage social observé sur des animaux soumis à des tâches de laboratoire comme des cas particuliers de conditionnement opérant ou classique. Aucune de ces approches traditionnelles n'avaient fourni beaucoup d'idées sur les processus complexes qui appuient souvent l'apprentissage animal social. En combinant les approches éthologiques à l'apprentissage social tel qu'il survient dans l'habitat naturel avec les techniques analytiques développées dans les laboratoires de psychologie, les chercheurs contemporains ont fait des progrès considérables dans la description des nombreuses façons par lesquelles les interactions sociales favorisent le développement animal. Les recherches de l'auteur sur les influences sociales en rapport avec la sélection de nourriture par les rats Norvégiens fournissent un exemple d'une telle approche "éthopsychologique" pour étudier l'apprentissage social animal.

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PART 1: A LITTLE HISTORY

We humans are profoundly social animals. The biological success of our species — our numbers, our worldwide distribution — depends in no small measure on our ability to acquire behaviour socially: to use and, over generations, to improve upon one another's responses to environmental challenge. Members of our species, however, are not unique in using the behaviour of others to guide their own responses to life's demands. Like us, various insects, fishes, birds, and mammals can exploit the behaviour of conspecifics to bias their own behavioural development in adaptive directions.

We humans are, apparently, exceptional in our spontaneous use of arbitrary signs and symbols to communicate with our fellows. We may well be unusual both in intentionally teaching others how to behave (Barnett, 1968; Ewer, 1969; Galef & Dalrymple, 1978) and in the extent to which we acquire motor skills by observing and then imitating our more accomplished fellows (Davis, 1973; Galef, 1988b; Roberts, 1941; Thorpe, 1963). However, it is only recently that evidence supporting even these relatively simple statements about differences in the processes supporting social learning by members of our own and other species has become available. For many decades, the processes used by animals and by humans to learn socially were assumed to be identical.

Did It All Begin With Gall?

Late in the first half of the 19th century, Franz Gall, father of phrenology, quoted with approval the following passage from the works of the French philosopher and naturalist Charles-George Leroy to show that animals (in this case foxes), like humans, used arbitrary sounds, "verbal language" (Gall, 1835, p. 26), to communicate ideas and emotions:

> It is certain from observation, that before having been able to instruct themselves by personal experience, the young foxes on leaving the burrow, for the first time, are more distrustful, and more cautious in the places where war is often made on them, than in places where the snares have never been spread. This observation, which is incontestable, proves absolutely the need they have of language; for, without it, how could they acquire the knowledge of proper precautions, which knowledge supposes a succession of facts known, of comparisons made, of judgments rendered? It appears then, that it is absurd to doubt, that brutes have among them a language, by means of which they transmit ideas, the communication of which is necessary to them. (Leroy, 1802, in Gall, 1835, p. 29)

To the modern reader, Leroy's views on the mechanisms of animal social learning and Gall's uncritical promotion of them (assuming, for the sake of argument, that naive young foxes do, in fact, behave as Leroy asserted they do) may suggest that both gentlemen were singularly thoughtless or gullible. It is, however, probably more reasonable to assume that the failure of Gall and of Leroy to provide a convincing explanation of the avoidance by naive, young foxes of areas containing snares arose not from thoughtlessness or gullibility, but from a lack of alternative hypotheses to explain the behaviour of foxes.

For the contemporary reader, aware of the existence of pheromones, in general (Wilson & Bossert, 1963), and of warning pheromones, in particular (von Frisch, 1941), or knowledgeable about the ways in which European blackbirds (Curio, Ernst, & Vieth, 1978) or rhesus monkeys (Cook, Mineka, Wolkenstein, & Laitsch, 1985) come to avoid potential predators, observations of social influences on avoidance are not evidence of an ability of animals to communicate using language. However, if, like Gall and Leroy working in the 19th century, we today knew of no means other than language for the transmission of information between individuals, then any evidence of animal communication would serve us, as it served Leroy and Gall, as evidence of human-like speech in nonhumans. Gall and Leroy did not lack intellectual prowess, they lacked alternative hypotheses with which to explain the behaviours in which they were interested.

Imitating Romanes

Attribution of social influences on the development of behaviour in animals to their use of language disappeared from the scientific literature in mid-19th century. Unfortunately, explanation of social learning by animals in terms of humanlike speech was replaced by an equally misleading, equally all-encompassing explanation of social influence on behaviour that proved considerably more difficult to reject than Leroy's idea that animals talk to one another about matters of importance.

Darwin, Wallace, Romanes, Morgan (for much of his life), and other, lesser known naturalists of the latter half of the 19th century treated learning by imitation as the primary way in which animals acquire adaptive behaviour. The ability of animals to learn by imitation was taken for granted. The only question to be asked was whether the ability to imitate had been exercised in particular instances of behavioural development (Morgan, 1896, p. 184).

Darwin's disciple and immediate intellectual heir in behavioural matters, George Romanes, was particularly quick to infer that animals were capable of "intelligent perception of the desirability of modification [in behaviour] on the part of certain individuals and to modify their actions accordingly" (Romanes, 1884, p. 229). According to Romanes (p. 219), "with animals as with men, original ideas are not always forthcoming at the time they are wanted, and therefore it is often easier to imitate than to invent."

Indeed, whenever Romanes (1882, 1884) saw evidence of social influences on learning in animals — whether in groups of newly hatched chicks learning to drink water, weanling lambs avoiding ingestion of toxic plants, or the acquisition of responses by birds of one species to the warning cries of another — he attributed the adaptive modifications of behaviour he described to learning by imitation. When a cat, resident in Romanes's household, learned to open the garden gate by jumping up and grabbing hold of the latchguard with one forepaw, depressing the thumb piece with the other, and simultaneously kicking at the gate post with her hind legs, Romanes (1882) assumed: first, that the cat had observed humans opening the gate by grasping the handle and moving the latch, second, that the cat had reasoned "If a hand can do it, why not a paw?" (Romanes, 1882, p. 422), and, finally, that the cat, motivated by this insight, had attempted to open the garden gate and succeeded.

Introspection had convinced Romanes (1882) that much of human behaviour was learned by imitation. Anthropomorphic inference led Romanes to generalize his introspections to explain acquisition of novel behaviours by animals, as he had explained acquisition of novel behaviours by members of his own species, in terms of learning by imitation (see Galef, 1988c, for further discussion).

Constraints on the Study of Animal Learning

In the century since Romanes (1882, 1884) published his classic volumes on comparative psychology, the anthropomorphism so common in 19th-century monographs on animal behaviour has been purged from the literature. Discussions of animal intentions and intelligent perceptions have been replaced by analyses in terms of stimuli, responses, and reinforcers. This reductionist approach to the analysis of behaviour, advocated by Morgan, Thorndike, and Watson, profoundly influenced not only interpretations of the results of animal learning studies but also their methods and subject matter. Anecdotal reports of cats and dogs learning complex motor skills by imitating their masters have been superceded by controlled experiments analyzing the factors influencing association formation in laboratory situations. The resultant changes in the focus of studies of animal learning generally, and of animal social learning particularly, have proven a major advance. However, as is often the case, progress was not entirely without cost.

The introduction, early in the present century, of experimental procedures for investigating association formation resulted in a precipitous shift in the subject matter of animal development studies. Interest in the development of behaviours exhibited by animals outside the laboratory (the centre of attention since the time of Aristotle) waned. Conversely, study of laboratory situations in which abstract processes of association formation could best be observed and dissected increased dramatically. This shift in locus of attention had a profound impact on the study of social learning by animals. Following Thorndike's (1898) explicit rejection, on theoretical grounds, of the possibility of learning by imitation in animals and failure both by Thorndike (1898) and by numerous other laboratory workers (see Holmes, 1911; Warden & Jackson, 1935; and Washburn, 1908 for reviews) to find convincing evidence of animal imitation, discussions of learning by imitation gradually disappeared from the behavioural literature. Such discussions were replaced by attempts to analyze instances of social learning, demonstrated in laboratory situations, as special cases of either classical or discriminant operant conditioning (for examples see Church, 1968; Miller & Dollard, 1941). Study of particular instances of apparent social learning observed outside the laboratory seemed unnecessary; in time, all instances of behaviour acquisition, whether individually or socially based, would be explicable in terms of general laws describing all association formation.

Meanwhile, in the world outside the learning laboratory, ducklings continued to follow their mothers, song birds went on singing their species-typical songs, and weaning animals continued to choose the same foods to eat as their more experienced fellows. The psychological community simply didn't pay attention to such occurrences. Those learning phenomena that could be explained easily within the framework provided by laboratory learning paradigms received careful study by numerous investigators. Those instances of animal learning that were more difficult to assimilate into either of the prevailing laboratory paradigms were largely ignored. Experimental, animal psychologists lost interest in carrying out analyses of instances of animal learning observed outside the laboratory, at least in part because successful study of learning in unconstrained situations required an approach quite different both from the informal anthropomorphizing of 19th-century naturalists and from the paradigm-bound examination of associative processes that dominated the study of animal learning.

An Alternative Zeitgeist

The development by European ethologists of a complementary framework to that provided by experimental psychology for the study of animal behaviour, in general, and animal learning, in particular, provided the background for a resurgence of interest in the study of behaviours that occurred outside the laboratory. Ethologists studied behaviours exhibited by members of particular species in interaction with their respective natural environments. Observations of such naturally occurring behaviours served ethologists as a focus for subsequent developmental, causal, and functional analyses. Consequently, analyses of the behavioural processes supporting particular instances of social learning observed in natural circumstances fit easily into ethologically oriented research programmes.

Further, ethologists were more eclectic than experimental psychologists in discussing processes supporting the acquisition of behaviour; ethologists had no particular commitment to operant or classical paradigms as explanatory systems; and they felt no compulsion to study animal learning in situations where it might occur "free from the helping hand of instinct" (Thorndike, 1911, p. 30). On the contrary, ethologists treated learning as an adjunct to instinctive behavioural sequences (Tinbergen, 1951).

Although ethologists both promoted analyses of the development of behaviours observed in uncontrolled environments and maintained an eclectic approach to the study of behaviour acquisition, they lacked a tradition of sophistication and rigour in the analysis of behavioural development, in general, and of animal learning, in particular. Of course, experimental psychologists had spent decades developing techniques that ethology lacked for the study of acquisition processes in animals. Hence, by the mid-1960s, the elements of a hybrid *ethopsychological* framework were available that permitted focus on the question of how naturally occurring behaviours might develop and that provided methods needed to arrive at satisfying answers. In particular, the question of how animals might use information acquired from others to guide their own behaviour in adaptive directions, a question that, at least implicitly, had been perplexing scientists for the better part of 2 centuries, was finally open to systematic investigation. The issue was no longer whether animals could imitate, but, rather, how one individual might use the behaviour of others to bias its own development in appropriate directions (Galef, 1989d).

PART 2: A PROGRAMME OF RESEARCH

For the past 20 years, my co-workers, my co-workers and I have been studying the role of social interaction in the development of adaptive patterns of food selection by Norway rats (*Rattus norvegicus*). The immediate goal of this research programme has been to determine the behavioural processes that cause one rat to direct its feeding behaviour towards the same foods that others of its social group are eating and to ignore potential foods that others of its social group are not eating. Equally important, we hoped to develop a general approach to studies of social learning that would be of use to future investigators of analogous behavioural phenomena.

My co-workers and I began, as any ethologist would, with field observations of a possible case of social learning. We brought the behavioural phenomenon observed in the field into the laboratory and, as any psychologist would, then tried to determine under controlled conditions how one animal influenced another's behaviour.

Problems Poisoning Norway Rats

More than 40 years ago, an applied ecologist who was an expert in the control of Norway rats discovered that when he used a single poison bait in a rat-infested area for several months, despite initial success, later acceptance of the bait was negligible. As might be expected, many members of the target population died as the result of eating the poisoned bait. Other rats chanced to eat sublethal amounts of bait, became ill, and learned not to eat any more of the bait that caused their illness. Most interesting to students of animal social learning, young born to rats that had learned to avoid the poison bait rejected the bait without even tasting it themselves. These juveniles fed exclusively on safe foods available in the territories of their respective colonies for as long as the adults that had learned to avoid the poison bait survived (Steiniger, 1950).

Steiniger's (1950) observations of naive, young rats totally avoiding a poisoned bait that members of their parent colony had learned to avoid is strikingly similar to Leroy's observation 150 years earlier of naive, young foxes acting uneasy in places where members of their parents' generation had encountered snares. Both Steiniger's and Leroy's (1802, cited in Gall, 1835) observations provide presumptive evidence of an important role of social learning in the development of an adaptive pattern of behaviour. In neither case, however, does simple observation provide much insight into the ways in which interactions with more knowledgeable conspecifics had influenced the behaviour of young animals.

A Laboratory Analogue

My co-worker, Mertice Clark, and I (Galef & Clark, 1971a) were fortunate in that the phenomenon described by Steiniger (1950) can be studied easily in colonies of wild Norway rats living in the laboratory in small (1 × 2 m) enclosures. By introducing nonlethal, nauseating concentrations of a mild toxin into Diet B, the more palatable of two diets (A and B) that we presented to our laboratory-maintained colonies for 3 hr each day, we were able to train adult colony members to avoid eating Diet B and to feed exclusively on the less palatable Diet A.

Soon, the adult members of our colonies had learned an aversion to Diet B. They would not eat Diet B even if offered unpoisoned samples of that diet, and we were able to remove the toxin from the portions of Diet B offered to colony members each day. Then we had to wait for weeks or months until our trained colonies produced litters and until the litters grew to an age when their members began to eat solid food. Finally we could observe the food choices of weanling rat pups raised in colonies that would eat only Diet A, the less palatable of two uncontaminated foods available to them.

As Steiniger (1950) would have predicted, for as long as the young were left in contact with adult colony members, juveniles raised in colonies which had been trained to avoid Diet B and to eat the less palatable Diet A ate only Diet A. During the weeks that we observed individual weanlings eating solid food, only a single pup of more than 200 raised in colonies trained to avoid diet B ate so much as a single mouthful of that diet.

The results of this first experiment were exceptionally clear. Adult wild rats could bias their young to eat a relatively unpalatable safe food (Diet A) and to ignore a more palatable, potentially dangerous food (Diet B). The question, of course, is how were adults influencing the behaviour of their offspring?

Steiniger (1950) had attributed the avoidance of poison bait, exhibited by the young wild rats he observed, to the effects of urine and feces deposited on baits by adults that had eaten sublethal portions of bait and learned to avoid it. He assumed that such scent marking by knowledgeable adult rats was necessary if naive weanlings were to avoid poisoned baits without incurring the risks associated with sampling them. However, when Clark and I conducted controlled experiments in which we offered samples of Diet B uncontaminated by adult droppings to young wild rats raised by colonies of adults trained to avoid Diet B, the young continued to avoid Diet B totally (Galef & Clark, 1971b). Apparently, our pups weren't avoiding Diet B because adults of their colony were marking that diet.

In fact, we could find no evidence that our rat pups actually learned to avoid foods that adults of their colony were avoiding. For example, when offered a choice between Diets A and B at weaning, rat pups reared by adult rats who were fed only Diet A and who were never exposed to Diet B ate only Diet A, just as did pups reared by adults that had been trained to avoid Diet B and to eat only Diet A (Galef & Clark, 1971b). The results of our experiments consistently indicated that, during interaction with adults, our wild rat pups were learning only to eat the foods that adults were eating, not to avoid foods that adults were avoiding (Galef, 1985a).

Previous research on the behaviour of wild rats suggested a way in which adult determination of the foods rat pups ate could result, indirectly, in adult determination of the foods pups avoided. Wild Norway rats are extremely hesitant to eat unfamiliar foods (Barnett, 1958; Galef, 1970). Consequently, presence of a familiar food can result in exclusion of other available foods from the diets of young wild rats. So, if we could determine how weanlings came to eat the food that the adults of their respective colonies were eating, we might also understand why weanlings avoided foods that adults were avoiding (Galef, 1985a)

How Time Flies

It still comes as something of a shock to me to realize that almost 20 years after first providing laboratory evidence that young rats can be influenced in their food selection by the learned feeding habits of adults of their species, students in my laboratory and I are still studying the ways in which social influence affects the food choices of young rats. Twenty years may seem to you, as it does to me, an inordinate amount of time to spend on such an apparently simple problem. Be assured, I have excuses for my failure to achieve a solution more rapidly: First, what appears to be a simple problem turns out to be quite complex. Rats do not have a single method of influencing one another's feeding behaviour. They have several independent methods, each of which presents a separate analytic problem. Second, the implications of the ability of rats to direct one another's feeding behaviour in adaptive directions turn out to be more far-reaching than I had anticipated, and working out those implications has taken considerable time and effort.

Mechanisms for Social Learning About Foods in Norway Rats

Over the years, my co-workers and I have described and analyzed four different ways in which adult Norway rats can bias their young to feed on one food rather than another. Each is discussed separately below:

1. Effects of the presence of adults at a feeding site. One of the simpler ways in which adult rats can induce their naive young to eat one food in preference to others is for the adults to eat only at locations where a particular food is to be found. The presence of adults at a feeding site attracts young to that site and causes the young to eat whatever food is present there. For example, both 19- and 25-day-old rat pups ate four times as much food from a food bowl with an anaesthetized female rat draped over its rim than from an identical bowl 1 m away which lacked an anaesthetized female (Galef, 1981b). Similarly, Clark and I observed each of nine, individually marked, wild rat pups eat their very first meals of solid food in a large enclosure; each ate that meal both while an adult was eating and at the same food bowl from which the adult was eating, not from a second food bowl 1.5 m away (Galef & Clark, 1971b). Thus, adults can bias weanlings to initiate feeding on a particular food simply by their presence at a site where that food is located. Such biasing of initial food intake toward a food that adults are exploiting can influence pups totally to avoid other, available foods that adults have not induced them to eat.

2. Effects of residual olfactory cues. Adult rats mark both the foods they are eating and the areas around those foods with residual olfactory cues that make marked foods or marked feeding sites more attractive than unmarked alternatives to juveniles seeking food. Galef and Heiber (1976) restricted either rat mothers and their young or groups of virgin female rats to one end of a 2 × 1 m cage for several days. Then, while these stimulus animals were absent from the cage, food-deprived juveniles were tested individually for 1-hr periods with identical bowls of food at each end of the cage. Individual weanlings took 70–90% of the food they ate from the end of the enclosure that had been soiled by other rats. Young rats also ate more food from a bowl that an experimenter had surrounded with rat excreta than from a food bowl in an unsoiled area. Some years later, Galef and Beck (1985) showed that adult rats spontaneously mark a feeding site they visited or food they ate, making each more attractive to other rats than identical, unmarked foods or sites.

Although effective in biasing the diet preferences of young in adaptive directions, the two behavioural mechanisms for communication of food selection described above are not very sophisticated. They are examples of the effects on feeding behaviour of a process that Thorpe (1963, p. 134) labelled *local enhancement*, that is, "apparent imitation resulting from directing the animals' attention to a particular object or a particular part of the environment." Instances in which adult rats directly communicate information to their young as to what foods should be eaten or avoided are, perhaps, of greater interest.

3. Flavour cues in mother's milk. The results of two sets of studies in my laboratory (Galef & Henderson, 1972; Galef & Sherry, 1973) as well as a variety of findings from other laboratories (e.g., see Martin & Alberts, 1979) are consistent with the hypothesis that: (a) The milk of a lactating rat contains cues reflecting the flavour of her diet, and (b) these flavour cues in mother's milk influence pups' selections of foods to eat at weaning.

Some of the most convincing evidence for the existence of flavour cues in mother's milk that reflect the flavour of the mother's diet came from studies in which rat pups nursing from a female rat eating Diet A were made ill by injecting them with LiCl after we had hand fed them a small quantity of milk expressed manually from a second lactating female eating Diet B. Tests at weaning showed that these pups developed aversions to Diet B, the diet fed to the lactating female from which we had taken the manually expressed milk (Galef & Sherry, 1973). Evidence of transmission of flavour cues through mother's milk has also been provided by artificially introducing a flavour into the milk of a mother rat by intraperitoneal injection, thus causing her pups to exhibit an enhanced preference at weaning for foods of the introduced flavour (LeMagnen & Tallon, 1968; Martin & Alberts, 1979).

In other studies, Galef and Henderson (1972) found that rat pups raised by mothers eating Diet B and fostered for 6 hr/day for 18 days to a lactating female eating Diet A showed an enhanced preference for Diet A at weaning, relative to pups fostered daily to maternal, nonlactating females eating Diet A. These last data suggest that pups not only detect the flavour of a lactating female's diet in her milk, but also exhibit a preference for diets of that flavour at weaning.

4. Effects of olfactory cues on the breath of adult rats. Galef and Wigmore (1983) and Posadas-Andrews and Roper (1983) discovered independently that after a naive, adult or juvenile rat (an observer) interacted for a few minutes with a conspecific that had recently eaten some food (a demonstrator), the observer would show a substantial enhancement of its preference for the diet that its demonstrator had eaten.

Considerable progress has been made in understanding the messages passing from demonstrators to observers which allow demonstrators to influence their respective observers' diet choices. To summarize the results of a lengthy series of studies, the data suggest that both olfactory cues (Galef & Wigmore, 1983) escaping from the digestive tract of demonstrator rats and the smell of bits of food clinging to the fur of demonstrator rats are each sufficient to allow observers to identify the foods that their respective demonstrators have eaten (Galef & Stein, 1985). However, simple exposure of observers to the smell or taste of a food is not, in itself, sufficient to enhance an observer's preference for that food (Galef, 1989b; Galef, Kennett, & Stein, 1985; Heyes & Durlach, 1990).

Observers' preferences for foods are increased by experience of the smell of a food in contiguity with rat-produced odours (Galef & Stein, 1985). These behaviourally active odours (semiochemicals) emitted by demonstrator rats, which increase observers' preferences for foods the semiochemicals are associated with, are probably volatile sulfur compounds like carbon disulfide, a chemical constituent of rat breath that, when added to a food, increases the preference of both rats and mice for that food (Bean, Galef, & Mason, 1988; Galef, Mason, Preti, & Bean, 1988; Mason, Bean, & Galef, 1989).

Implications of Social Learning for the Development of Adaptive Foraging Behaviours

The evidence reviewed briefly above indicates that rats can be influenced in their choices of feeding sites and of foods by the feeding behaviour of other rats. In the present section, I discuss evidence suggesting that, outside the laboratory, information garnered by naive rats from their fellows as to the foods they have eaten could be used by the naive to find nutritionally adequate foods, to identify toxins, and generally, to forage more efficiently than would be possible in the absence of socially acquired information.

What to Eat: In a recent experiment, Beck and Galef (1989) allowed individual weanling rats to choose among four distinctively flavoured foods for 144 consecutive hr. Three of these foods contained inadequate levels of protein (4.4%), and one, the least palatable of the four, provided ample protein (17.5%) for normal growth. Beck and I found, as had others before us (Kon, 1931; Scott & Quint, 1946; Scott, Smith, & Verney, 1948; Tribe, 1954, 1955), that young subjects performed poorly in such a situation. None of the juvenile subjects in our experiments was able to develop a preference for the protein-adequate food in 6 days; each pup lost weight, and each appeared well on its way to a premature demise, if we had not terminated the experiment. Weanling rats faced with the same food-selection problem, while in the presence of adults previously trained to eat the protein-rich alternative, had no difficulty in focussing their intake on the protein-rich food and grew rapidly in the experimental situation (Beck & Galef, 1989). Thus, in a situation in which individual, naive, young rats found it impossible to select a nutritionally adequate food from among inadequate alternatives, the naive could use information acquired from others as to the food those others were eating to identify an adequate food and to achieve normal rates of growth and development.

What Not to Eat: New recruits to a population (recent immigrants or naive juveniles) need not only to find and ingest nutritionally adequate foods, they must also avoid ingesting debilitating quantities of any toxic substances they encounter. In the search for needed nutrients, a naive individual might have to sample broadly among unfamiliar, ingestible substances. By sampling one unfamiliar substance at a time and by waiting long enough between meals of unfamiliar food to evaluate independently the postingestional consequence of each (Rozin & Kalat, 1971), a naive individual could determine whether each unfamiliar substance it ingested was toxic (Zahorik & Houpt, 1981). There is, however, little evidence that rats actually sample among several unfamiliar foods so as to permit their independent evaluation. On the contrary, laboratory data suggest that, when offered a number of unfamiliar foods to eat, even genetically wild Norway rats will eat several different unfamiliar foods during their first bout of feeding that includes any unfamiliar foods (Barnett, 1956; Beck, Hitchcock, & Galef, 1988; Rozin, 1969).

Information about the foods others are eating can provide naive individuals with an alternative to careful sampling for identification of toxic substances. Galef (1986b, 1986c, 1987, 1989d, in press-a), found that naive rats that had interacted with recently fed conspecifics were less likely to form aversions to foods that the other rats had eaten than they were to form aversions to totally unfamiliar foods. For example, naive observer rats that interacted with recently fed demonstrator rats before eating two unfamiliar foods and becoming ill learned an aversion to whichever of the foods their respective demonstrators had not eaten (Galef, 1986c, 1987). Further, a substantial proportion of rats that had formed an aversion to a food as a result of previous association of that food with toxicosis totally abandoned their learned aversion following exposure to other rats that had eaten the averted food (Galef, 1985b, 1986b).

If, as seems likely, it is usually the case that unfamiliar substances that others are eating are less likely to be toxic than are unfamiliar substances that others are not eating, then social influences on taste-aversion learning could be an important source of information both about whether illness was food related (Domjan & Galef, 1983; Galef, in press-a) and about which of several recently eaten foods was most probably illness inducing (Galef, 1986c, 1987).

Where to Eat: Galef, Mischinger, and Malenfant (1987) found that rats that were familiar with a maze would spontaneously follow trained rats through the maze to food. They also found that rats trained to follow leader rats through a maze were more likely to follow leaders that had just eaten a familiar, safe food than to follow leaders that had just eaten a food that the potential followers had learned to avoid eating. Thus, hungry rats exhibited both a readiness to follow others to feeding sites and an ability to select others to follow on the basis of the desirability of the foods those others had eaten.

Further, Galef (1983) and Galef and Wigmore (1983) have shown that rats, familiar with the locations at which particular foods were sometimes to be found but ignorant as to which food was currently available, could use information garnered from a recently fed conspecific to decide where to look for food. After interacting with an "informer" rat that had just eaten cinnamon-flavoured food, a subject rat went to the location where it had previously learned that cinnamon-flavoured food was to be found. After interaction with an informer rat that had just eaten cheese-flavoured food, the same subject went to the location where it had previously learned that cheese-flavoured food was to be found (Galef, 1983; Galef & Wigmore, 1983).

Summary: The ability of rats to identify substances that others of their species have eaten provides the naive with information of use in the development of adaptive feeding patterns. As described in the preceding section, Norway rats have available a range of ways in which to discover which substances others of their social group have eaten. As discussed in the present section, one rat can exploit others as sources of information to facilitate its location of foods, its selection of nutritious foods from among alternatives, and its learning of aversions to toxic substances. Such socially acquired information may be of fundamental importance in the development of adaptive feeding repertoires by wild Norway rats living outside the confines of the laboratory.

PART 3. CONCLUSIONS

Analysis of the behavioural processes supporting social learning proved more difficult than its early students could have anticipated. Alone, neither the observational approach employed both by early naturalists and by ethologists nor sophisticated analyses of social influences on the acquisition of behaviours typically studied in psychological laboratories was adequate for determining what animals could learn socially or how social learning proceeded (Galef, 1989c). In recent years, integrated, ethopsychological approaches to the study of social learning have provided a better understanding of social learning in animals than either traditional psychological or traditional ethological approaches pursued in isolation.

Behaviours to Study

The ethological orientation has focussed attention on the role of social learning in the development of behaviours that occur in natural habitat, that contribute to fitness, and that have been shaped by natural selection (Galef, 1989a). The ethological orientation has proven particularly valuable in the study of social learning by animals because the acquisition processes supporting social learning are often both situation- and species-specific. Social learning is often, in Thorndike's (1911, p. 78) words, ''the indirect result of instinctive acts'' of various kinds. On the other hand, both the species and tasks used by psychologists in laboratory investigations of associative learning were intended to permit study of association formation, again in Thorndike's (1911, p. 30) words, ''free from the helping hand of instinct.''

To the extent that students of association formation were successful in designing truly arbitrary laboratory tasks minimizing the impact of instinctive behaviour on performance, associationists may have designed, unintentionally, situations in which the role of social influence on behaviour would also be minimized. Consequently, observation of the development of behaviour in free-living animals should be a more useful starting point for the study of animal social learning than behaviour exhibited in laboratory situations that were designed, albeit inadvertently, to reduce the probability that social influences on learning would occur in them.

Methods of Study

If much of animal social learning is both species- and situation-specific, then analyses of the behavioural processes supporting social learning in terms of general learning processes, of the same level of abstraction as those used to discuss individual learning, are unlikely to prove successful. Before the fact, what general theory could have predicted that the dances of honeybees contain useful information about the locations where pollen and nectar are to be found, that the mobbing calls of European blackbirds act as powerful unconditioned, aversive stimuli in the social learning of avoidance of potential predators (Curio et al., 1978), or that exposure to the breath of a recently fed rat causes changes in the food preferences of conspecifics? Observations of bees recruiting their fellow foragers to feeding sites, of jackdaws starting to mob previously ignored objects, and of rats avoiding poison baits without previous experience of those baits required explanation. It is in the open-ended attempt to explain the causes of such phenomena that the unpredictable richness and complexity of the social processes guiding learning were revealed.

On the other hand, by itself, observation offers no royal road to success in studies of social learning. Observations in uncontrolled environments provide neither entirely convincing evidence of a role of social interaction in behavioural development nor insight into the behavioural processes that might support social learning in natural circumstances.

Successful studies of social learning processes depended on the synthesis of two historically distinct traditions in the study of behaviour: observation in natural circumstances to identify promising areas for investigation and sophisticated analytic procedures in controlled situations to determine the causes and potential functions of the behaviours under study.

Empirical Contributions to the Field of Social Learning

I began this essay with a brief discussion of Leroy's rather unconvincing answer to the question of why the young foxes he observed were wary the very first time they approached places where snares had previously been set to catch their parents. I suggested that Leroy's failure to provide a useful analysis of the causes of this wariness in young foxes resulted from his ignorance of the broad range of behavioural processes that might, in principle, have produced the socially transmitted behaviour he was trying to explain. Indeed, the history of the study of animal social learning during the decades since Leroy's pioneering attempt to analyze a socially transmitted behaviour seen in nature could be characterized as a gradual filling in of the gaps in Leroy's knowledge. Increasingly sophisticated laboratory investigations of social learning processes have provided awareness of the many different ways in which social interactions can direct behavioural development in adaptive directions (Galef, 1988b, 1989a, in press-b).

In such a view of progress in the field of social learning, lasting empirical contributions to the area are those that increase the number of processes known to play a role in social learning. Consequently, the success of any laboratory analysis of an instance of animal social learning should be measured not only by its provision of insight into the particular instance of social learning it was undertaken to investigate, but also by its contribution to understanding of social learning processes more generally. In particular, the success of the research in which my laboratory has been engaged for the past 2 decades (reviewed in Part 2 above and in Galef, 1977, 1986a, 1988a, in press-c) should be judged not only in terms of its contributions to the understanding of the phenomena that our experiments addressed directly (i.e., the feeding, poison avoidance, and foraging behaviour of rats as discussed in Galef 1981a, 1988a, in press-c; Galef & Beck, in press), but it should also be assessed with respect to its contributions to more general understanding of social learning processes. In the latter respect, 20 years of research in my laboratory may not have accomplished much. True, we have provided evidence that information influencing food selection can be communicated from mammalian mothers to their young via mother's milk (Galef & Henderson 1972; Galef & Sherry, 1973) and from one adult animal to another via odour cues carried on their breath (Galef & Stein, 1985; Galef & Wigmore, 1983; Valsecchi & Galef, in press). These are, however, limited discoveries, relevant only to social influences on feeding behaviour.

On the other hand, our finding that exposure of rats to an odour in the presence of a conspecific can have very different effects on subsequent behaviour with respect to that odour than does simple exposure to the same odour (Galef, 1982, 1989b; Galef & Kennett, 1987; Galef & Stein, 1985; Heyes & Durlach, 1990) may apply to acquisition of responses to a broad range of stimuli. If it should prove to be the case that, in general, exposure to stimuli in a social context has effects on behaviour markedly different from exposure to the same stimuli in isolation (e.g., see Baptista & Petrinovich, 1986), then our research may have made a fundamental, empirical contribution to the understanding of social learning processes.

Theoretical Contributions to the Study of Social Learning

In the preceding section, I characterized the history of the study of animal social learning as a steady accumulation of knowledge concerning the many ways in which social interactions can shape behavioural development. There is, however, an alternative, less charitable, and not entirely inaccurate description of the history of the field. One might describe the last 100 years of laboratory research in the area of animal social learning as an unending quest by some to provide evidence that learning by imitation occurs in animals and by others to demonstrate that any proposed instance of imitation learning by animals can be explained in terms of less complex learning processes.

Surely, the question of whether animals can learn by imitation is theoretically important. Its definitive answer would help to resolve some venerable questions concerning the relationship of animal to human mind (Galef, 1985c, 1986d, 1988c). Further, there can be no doubt that a robust, replicable demonstration of imitation learning, particularly by members of a nonprimate species, would be a major empirical contribution, allowing otherwise impossible analyses of cognitive processes in animals. The field may well be on the verge of providing such demonstrations (e.g., see Heyes & Dawson, 1990, or Palameta, 1989).

There is, however, surely more to the study of social learning in animals than determining whether or not animals can learn by imitation. Learning by imitation is only one of a number of possible ways in which social interaction can influence behavioural development (Galef, 1988b). Indeed, the difficulty of demonstrating imitation learning in animals under controlled conditions suggests that such learning is not a major factor in the normal behavioural development of nonhuman species.

I have argued elsewhere (Galef, 1984) that the future of laboratory studies of animal learning lies in providing explanations of the acquisition of adaptive behavioural repertoires by animals living in natural circumstances. Single-minded focus on the question of whether animals can learn by imitation can only interfere with further progress in achieving this broader goal.

The research programme my laboratory has pursued, analyzing social influences on food selection in rats, demonstrates that extended laboratory investigations of social learning processes can be undertaken without focus on the question of whether animals are able to imitate. Our approach, characterized above as ethopsychological and elsewhere (Galef, in press-b) as developmental, exemplifies a general strategy for analysis of social learning phenomena (explored at length in Galef, 1976, 1988b, 1989a) that seems useful in describing and discussing the development of behaviour in free-living animals (for recent examples see Boinski & Fragaszy, 1989; Galef, in press-d; Hauser, 1988).

It is, of course, too early to know whether a developmental/ethopsychological approach to the study of social learning will have a broad or lasting impact on the field. It is my hope that the example provided by the research programme carried out in my laboratory will contribute to a reorientation of laboratory investigations of social learning phenomena. Studies of social learning have the potential to make fundamental contributions to our understanding of processes supporting the development of adaptive behavioural repertoires in free-living animals. Such studies should not be seen as relevant only to the decades-old debate between behaviourist and cognitivist students of animal learning as to how best to conceptualize associative processes.

There is already laboratory evidence that social learning can play an important role in the development of song in passerine birds (Baptista & Petrinovich, 1986; Marler & Tamura, 1964; West & King, 1986), of patterns of food preference in both rodents and birds (Galef, 1988a; Mason & Reidinger, 1981, 1982), and of avoidance of predators by birds and monkeys (Cook et al., 1985; Curio et al., 1978). The challenge for the future, as in the past, will be to extend understanding of the ways in which social interactions contribute to the development of adaptive behavioural repertoires in animals and, thus, to provide satisfying answers to questions of the type first posed by Charles-George Leroy in 1802.

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